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Photosynthesis, growth, and yield of *Paeonia ostii* in tree-based agroforestry systems

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Abstract

Paeonia ostii T. Hong & J.X. Zhang, an emerging oil crop, was intercropped with 3-year-old plantations of pawpaw [*Chaenomeles sinensis* (Thouin.) Koehne], Chinese toon (*Toona sinensis* Roem.), and walnut (*Juglans regia* L.). In order to achieve a better production system, we studied the effects of intercropping on the photosynthesis, growth, and yield of *P. ostii*. The results showed that different pattern of agroforestry systems changed microclimatic and growing site conditions in comparison to the control treatment. The correlation analysis demonstrated that both similarities and differences were found in relationship between net photosynthetic rate (P_N) and main ecophysiological factors at different treatments. Agroforestry systems significantly reduced transpiration rate and increased water-use efficiency (WUE), maximal quantum yield of PSII photochemistry, chlorophyll (Chl) *a* and total Chl contents, whereas there were no differences between P_N, intercellular CO_2 concentration, photochemical efficiency of PSII in the light, and plant height in these systems. The obviously exponential relationship between P_N and PAR during a day were observed in Chinese toon and walnut treatments. The highest effective quantum yield of PSII photochemistry, electron transport rate, and photochemical quenching coefficient were observed in walnut treatment. The higher WUE and SPAD value, the thinnest stem, the biggest crown, the lowest stomatal conductance, and Chl *a*/*b* ratio as well as the fewest pods and harvest seed yield were observed in pawpaw treatment. In addition, there was a significant correlation between SPAD value and Chl (*a*+*b*) of *P. ostii* in agroforestry system. This study could be an important contribution for the science of land management in oil peony and other understory crops.

Additional key words: intercropping systems; land management; morphological traits; photosynthetic characteristics.

Introduction

With the rapid development of Chinese economy and constant improvement of living level, problem of feeding the population has been basically solved, whereas fats and oils are more demanding than ever before. Consequently, researchers have targeted plant sources to explore their uses and functional properties with the goal of developing improved varieties of edible oils that can withstand future challenges (Cheng *et al*. 2016).

Paeonia ostii T. Hong & J.X. Zhang (Paeoniaceae), as an emerging oil crop, has a high potential in the production of oil. The plant is a perennial hardy shrub widely distributed in Henan and Anhui provinces of China. *P. ostii* is the parent of two medicinal varieties of tree peonies, namely, 'Feng Dan Bai' (Phoenix White) and 'Feng Dan

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Abbreviations: C_a – CO_2 concentration in air; Chl – chlorophyll; C_i – intercellular CO_2 concentration; E – transpiration rate; ETR – electron transport rate; F_0 – minimal fluorescence yield of the dark-adapted state; F_0' – minimal fluorescence yield of the light-adapted state; F_m – maximal fluorescence yield of the dark-adapted state; F_m' – maximal fluorescence yield of the light-adapted state; F_s – steady-state fluorescence yield; F_v/F_m – maximal quantum yield of PSII photochemistry; F_v'/F_m' – photochemical efficiency of PSII in the light; g_s – stomatal conductance; NPQ – nonphotochemical quenching; P_N – net photosynthetic rate; q_P – photochemical quenching coefficient; RH – relative humidity; T_{air} – air temperature; T_{leaf} – leaf temperature; WUE – water-use efficiency (= P_N/E); Φ_{PSII} – effective quantum yield of PSII photochemistry.
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Fen' (Phoenix Pink) which are grown for the bark of their roots, used as an antispasmodic throughout Asia (Surhone *et al*. 2010). Recently, the plant has been also recognized as underutilized woody oil-seed plant with a considerable potential for edible oil production. Compared to established oil crops, this plant presents a competitive agronomic performance, because the plant has a higher seed yield and unsaturated fatty acid content, especially of the α-linolenic acid, essential for human life (Kim *et al*. 2014, Yang *et al*. 2017). Moreover, seed oil of *P. ostii* is the versatile oil and is not limited to food, but widely used in oleochemicals, cosmetics, and pharmaceuticals (Han *et al*. 2014). In 2011, peony was approved as the new edible seed oil by the Ministry of Health in China. Development of peony oil tree planting contributes to meet increasing demand for fats and oils and holds future challenges, such as climate change, sustainability, and food security (Peng *et al*. 2017). This species is propagated by seeds and its seedling stage takes two years from sowing to planting. Vegetative growth is dominant at the juvenile stage and continues from 3rd to 5th year of its growth. Since only few flowers and fruits develop at that time and rows become full of weeds, substantial benefit from the plantation is negligible during this period. In addition, wild *P. ostii* is distributed under forest cover and is a shade-tolerant species (Hong *et al*. 2004, Tang *et al*. 2017). Therefore, agroforestry can offer a convenient strategy for promoting its cultivation and conservation.

Agroforestry, a multifunctional working landscape, can be a viable land-use option that, in addition to alleviating poverty, offers a number of ecosystem services and environmental benefits (Jose 2009). Obvious 'midday depression of photosynthesis' of *P. ostii* was observed in monoculture systems at noon, especially in summer, whereas moderate shading treatment could relieve effectively this phenomenon and improve the yield (Bi *et al*. 2011, Tang *et al*. 2017, Han *et al*. 2018). Previous studies also suggested that the forest margin and forest gap with appropriate shade were the most suitable growing environment for oil tree peony (Zhou *et al*. 2010, Zhang *et al*. 2014). Shade trees could reduce the stress by ameliorating adverse climatic conditions and nutritional imbalances, while they may compete for growth resources (Beer *et al*. 1997). With these potential benefits for tree-based agroforestry systems in mind, in order to maximize the potential benefits of crop, the reasonable choice of shade trees could avoid competitive interactions between trees and crops for nutrients, moisture, and light. Although many studies on *P. ostii* in tree-based agroforestry systems have been carried out in recent years, the results mainly focused on cultivation techniques and cost-benefit analysis (Xiang and Zhu 2016, Xu *et al*. 2017). There were few data available regarding the physiological and ecological characteristics and their relationship within agroforestry systems in summer that is the fruit developing and mature phase of this species. Considering the long-term history of cultivation in China, the objective of the present research was to study the *P. ostii* intercropping with trees of other species in order to achieve a better production system.

Materials and methods

Plant materials and site description: This study was conducted in July 2017 in an open experimental field (0.25 ha in area, 34°55'25"N, 113°37'36"E, 100 m a.s.l.) located in Zhengzhou the Yellow River National Wetland Nature Protection Zone, Zhengzhou, Henan Province, China. The typical north temperate continental monsoon climate of this region produces hot rainy summer, cold dry winter, and four distinct seasons. Mean annual temperature is 14.3°C and the annual mean rainfall is 640.9 mm. The average frost-free period is approximately 209 d and the mean annual light time is 2,400 h. The soil type of study area is sandy barren soil. The top soil layer (0–20 cm) at the studied field contained 5.10% total organic matter and 37.65 mg(available nitrogen) kg^{-1}. In the experimental fields, 0.06 kg m^{-2} of compound fertilizer ($NH_4H_2PO_4$) was applied for all treatments on 20 March (before florescence), 20 May (after florescence), and 20 September (abscission period) every year, respectively, and an irrigation followed. Otherwise, water came mainly from precipitation.

In the experiment, 2-year-old oil tree peony (*P. ostii*) cultivated seedlings, 'Feng Dan Bai', were transplanted in the field in October 2013. Three indigenous tree species, pawpaw [*Chaenomeles sinensis* (Thouin.) Koehne], Chinese toon (*Toona sinensis* Roem.), and walnut (*Juglans regia* L.), were planted in the spring 2014, with a row spacing of 3 m and between row spacing of 3 m. The tree rows were oriented north-south. Buffering zones, 5 m wide of *P. ostii* monoculture, were set between two treatments. *P. ostii* monoculture was considered as the control material during the experiment. *P. ostii* was planted at spacing of 0.4 m within rows and 0.5 m between rows of each treatment (pawpaw, Chinese toon, walnut, and control treat-

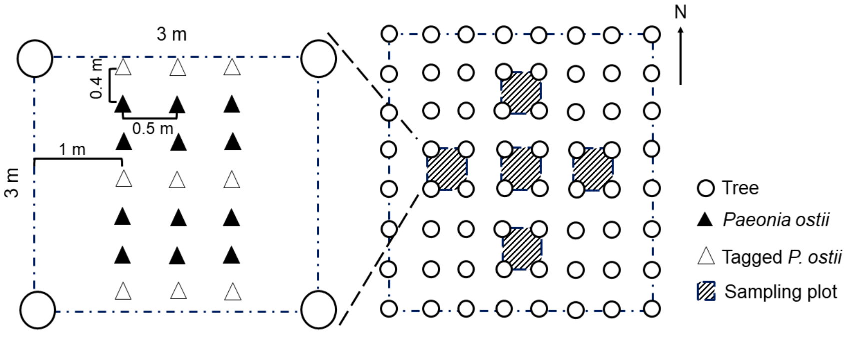

Fig. 1. Location of sampling plots (*shaded boxes*), trees (*circle*), *Paeonia ostii* (*filled triangle*), and tagged *Paeonia ostii* (*unfilled triangle*) between rows of trees.

ments). Nine tagged *P. ostii* plants in each sampling plot were research objects (Fig. 1). At each time of sampling, a single leaf from the upper *P. ostii* canopy was used.

In order to harvest the fresh young leaves and shoots of Chinese toon next spring, coppice management was carried out every winter. We pruned pawpaw and walnut trees every spring to promote the formation of flower buds. The characteristics of selected pawpaw, Chinese toon, and walnut trees intercropped with oil tree peony were variable. In general, the walnut trees were taller and had the thicker stem diameter than that of the pawpaw trees and Chinese toon trees (Table 1S, *supplement*). Crown dimensions also differed for the three species, with live crown depths and crown widths of walnut trees being greater than those of Chinese toon and pawpaw trees. The crown of Chinese toon trees was closer to the ground.

Leaf gas exchange and chlorophyll (Chl) fluorescence parameters: The portable photosynthesis system (*LI-6400XT*, *LI-COR Inc*., Lincoln, NE, USA) was used to determine the net photosynthetic rate (P_N), transpiration rate (E), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) of *P. ostii* upper leaves. The water-use efficiency (WUE) was obtained by the ratio of P_N to E. PAR, air temperature (T_{air}), leaf temperature (T_{leaf}), relative air humidity (RH), and CO_2 concentration in air (C_a) were also measured concurrently with the quantum sensor, thermistors, H_2O analyzer, and CO_2 analyzer present on the *LI-6400XT* photosynthesis system. The diurnal photosynthetic course was measured from 8:00 to 18:00 h with 1-h interval during three successive sunny days in middle of July.

Parameters of Chl fluorescence of *P. ostii* upper leaves were measured *via* a pulse-amplitude modulated (PAM) fluorometer (*Li-6400XT* with *6400-40* fluorescence leaf chamber, *LI-COR Inc*., Lincoln, NE, USA) during successive sunny days from 9:00 to 11:00 h in July. Initial fluorescence (F_0) and maximal fluorescence (F_m) were determined after 30-min dark adaptation at open air temperatures. The maximum photochemical efficiency of PSII (F_v/F_m) was calculated as $F_v/F_m = (F_m - F_0)/F_m$. The minimum fluorescence in the light (F_0'), maximum fluorescence (F_m') in the light and steady-state fluorescence (F_s) were determined after being adapted by more than 30-min PPFD of 1,200 μmol $m^{-2} \cdot s^{-1}$. The photochemical efficiency of PSII in the light (F_v'/F_m'), actual photochemical efficiency of PSII in the light (Φ_{PSII}), electron transport rate (ETR), photochemical (q_p), and nonphotochemical quenching coefficients (NPQ) were calculated based on the respective equations: $F_v'/F_m' = (F_m' - F_0')/F_m'$; $\Phi_{PSII} = (F_m' - F_s)/F_m'$; ETR = PPFD × Φ_{PSII} × 0.85 × 0.5; $q_p = (F_m' - F_s)/(F_m' - F_0)$, NPQ = $(F_m - F_m')/F_m'$.

Chl pigments and SPAD value: Chl concentration of upper leaves was estimated by biochemical methods (Arnon 1949) using 1 g of finely cut fresh leaves collected in mid-July. The sample was ground to a fine pulp with the help of a mortar and pestle and 20 mL of 80% acetone was added to it. This paste was centrifuged for 5 min at 5,000 rpm. The supernatant was transferred to a 50-mL beaker. The residue was then ground again with 20 mL of 80% acetone, centrifuged for 5 min at 5,000 rpm and the supernatant was transferred to the same beaker. The mortar and pestle were washed with 80% acetone and the clear washing were collected in the beaker. The volume was made up to 100 mL by adding extra 80% acetone. This was repeated for all the leaf samples. The absorbance (*Hitachi U-1900 UV-Vis Ratio Beam*, *Hitachi High Technologies*, Japan) of the extract solutions was read at 645 and 663 nm against the solvent (80% acetone) as blank. Pigment concentrations were calculated using the following equations:
Chl $a = 12.7\ A_{643} - 2.69\ A_{645}$, Chl $b = 22.9\ A_{645} - 4.68\ A_{663}$. A = absorbance at specific wavelengths.

The portable chlorophyll meter *SPAD 502* (*Konica Minolta Sensing*, *Inc*., Japan) measurements were performed on tagged leaves to estimate foliar Chl and total nitrogen (N) status.

Growth and yield: The stem diameter at 10 cm above the ground, plant height (from ground to the highest leaf), and crown width (mean diameter of crown) of *P. ostii* were measured with the help of a measuring tape and the number of pod per plant was counted in July. At maturity, early August, seed yield of every treatment was harvested. The harvested seeds were shade-dried for 30 d and then 1,000-seed mass and yield per ha were measured.

Statistical analysis and mapping: Statistical analyses were made using the *SPSS v. 20* software package. One-way analysis of variance (*ANOVA*) was used to test averages. Significant differences between treatments means were accessed using *Tukey*'s HSD at $P<0.05$. Correlation analysis was evaluated at $P<0.05$ and $P<0.01$. All measurements shown were the mean ± standard deviation (SD). All maps were generated by using *OriginPro v. 8.0*.

Results

Diurnal variation of PAR and T_{air} in the different treatments was shown in Fig. 1S (*supplement*). A similar diurnal variation of T_{air} was observed in all treatments. A similar diurnal variation of PAR was also observed in all treatments, except pawpaw treatment that showed an obvious decrease at 11:00 h followed by an increase, and PAR dropped rapidly from 13:00 to 17:00 h in all treatments.

For daily averages of main environmental factors, control and walnut treatments showed higher T_{air} and T_{leaf} than other treatments (Table 1). The lowest C_a was observed in the control treatment, while the highest C_a in walnut treatment. RH in Chinese toon and walnut treatments were higher than that in the other treatments. The total solar radiation reaching the upper parts of *P. ostii* canopies in different agroforestry systems was lower than that in the control treatment. In comparison with control treatment, pawpaw tree canopies incepted 46.6% of PAR.

The daily averages of leaf gas-exchange parameters of *P. ostii* in July by different treatments were shown in Table 1. Treatment differences for P_N and C_i were not observed. The g_s in pawpaw treatment was the lowest,

Table 1. Treatment differences for daily averages of leaf gas exchange and environmental parameters of control, pawpaw, Chinese toon, and walnut plots. Values are means ± SD, *n* = 45. *The same letters* indicate no significant differences ($P<0.05$) according to *Tukey*'s test. C_a – CO_2 concentration in air; C_i – intercellular CO_2 concentration; E – transpiration rate; g_s – stomatal conductance; P_N – net photosynthetic rate; RH – relative humidity; T_{air} – air temperature; T_{leaf} – leaf temperature; WUE – water-use efficiency.

Parameter	Control	Pawpaw	Chinese toon	Walnut
T_{air} [°C]	34.91 ± 0.20^a	33.86 ± 0.14^b	33.24 ± 0.17^c	34.52 ± 0.12^a
T_{leaf} [°C]	34.66 ± 0.25^a	33.73 ± 0.17^b	33.48 ± 0.19^b	34.58 ± 0.19^a
C_a [μmol(CO_2) mol^{-1}]	399.33 ± 1.34^b	401.06 ± 1.08^{ab}	401.59 ± 1.43^{ab}	404.36 ± 0.76^a
RH [%]	44.18 ± 0.79^b	45.72 ± 0.46b	49.96 ± 0.60^a	49.29 ± 0.75^a
PAR [μmol(photon) m^{-2} s^{-1}]	$1,303.51 \pm 64.42^a$	696.21 ± 73.76^c	$1,069.32 \pm 69.10^b$	$1,055.69 \pm 38.80^b$
P_N [μmol m^{-2} s^{-1}]	9.84 ± 0.30^a	9.54 ± 0.54^a	9.86 ± 0.41^a	10.10 ± 0.51^a
g_s [mol(H_2O) m^{-2} s^{-1}]	0.20 ± 0.01^{ab}	0.18 ± 0.01^b	0.22 ± 0.01^a	0.19 ± 0.01^{ab}
C_i [μmol(CO_2) mol^{-1}]	285.70 ± 3.59^a	287.20 ± 4.22^a	294.81 ± 2.87^a	285.78 ± 5.53^a
E [mmol(H_2O) m^{-2} s^{-1}]	5.37 ± 0.27^a	4.19 ± 0.16^b	4.24 ± 0.22^b	4.37 ± 0.17^b
WUE [μmol(CO_2) mmol(H_2O)$^{-1}$]	1.93 ± 0.06^c	2.47 ± 0.09^a	2.20 ± 0.08^b	2.37 ± 0.14^a

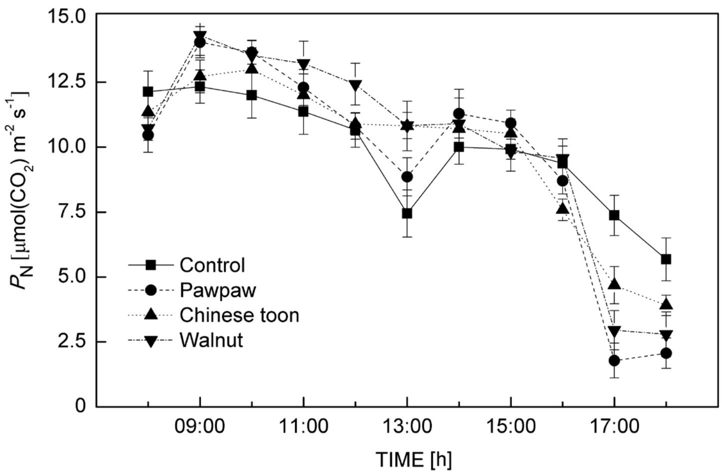

Fig. 2. Diurnal variation of net photosynthetic rate (P_N) of *Paeonia ostii* for control, pawpaw, Chinese toon, and walnut plots. Vertical bars represent SD (*n* = 45).

while that in Chinese toon treatment was the highest. The significant differences for E were between control and the other treatments, and higher WUE was observed in walnut treatment. The effect of different treatments on the diurnal variation of *P. ostii* P_N was divided into two situations (Fig. 2). Diurnal variation of P_N of *P. ostii* was found for control, pawpaw, Chinese toon, and walnut plots. Unimodal curves were observed in Chinese toon and walnut treatments, while bimodal curves were observed in control and pawpaw treatments. P_N of *P. ostii* in Chinese toon and walnut treatments did not show obvious 'midday depression of photosynthesis', while the phenomenon was observed in control and pawpaw treatments between 12:00 and 14:00 h.

The obviously exponential relationship between P_N and PAR during a day were observed in Chinese toon and walnut treatments (Fig. 3). However, the range of P_N in pawpaw and monoculture treatments was narrow throughout the day except for a few outliers in pawpaw treatment, where its P_N was more concentrated in the range of 8–16 μmol m^{-2} s^{-1} and PAR was below 1,600 μmol(photon) m^{-2} s^{-1}.

The parameters of Chl fluorescence under different treatments in July were summarized in Table 2. F_v/F_m illustrated a difference between control and the other treatments, while no difference was found for F_v'/F_m' in all treatments. The Φ_{PSII}, ETR, q_P, and NPQ value in control treatment was lower than that of intercropping systems. In comparison with monoculture and walnut intercropping system, pawpaw and Chinese toon intercropping systems significantly improved Chl *a*, *b*, Chl (*a*+*b*) contents, and SPAD value of *P. ostii* leaves. The lowest Chl *a*/*b* ratio was observed in the pawpaw treatment.

Correlation analysis of *P. ostii* P_N and environmental or physiological parameters was presented in Table 3. PAR and g_s positively correlated with P_N in all treatments. C_i and T_{leaf} showed highly significant negative and positive correlation with P_N in agroforestry systems, respectively. E and T_{air} had no correlation with P_N in Chinese toon treatment. The highly significant correlation between WUE and P_N was observed in pawpaw and walnut treatments. RH in pawpaw treatment had significantly negative correlation with P_N. However, C_a and ETR had no correlation with P_N in any treatment.

Table 4 showed the relationship of SPAD value and Chl content. Chl (*a*+*b*) showed significant positive correlation with SPAD value in agroforestry systems, while the negative correlation in control.

The stem diameter, 10 cm above ground, in pawpaw treatment was lower than that of the other treatments, while pawpaw treatment showed the biggest crown width (Table 5). Plant height did not show any difference for all the treatments. Compared to pawpaw intercropping treatment, Chinese toon and walnut treatments significantly increased pod number per plant. In addition, 1,000-seed mass in Chinese toon and walnut treatments was 11.0 and 5.0% higher than that of the control, respectively. Seed yield per ha in Chinese toon and walnut treatments was 54.5 and 18.9% higher than that of control, respectively. However, 1000-seed mass and seed yield in pawpaw treatment significantly decreased by 8.5 and 63.3% in comparison with control treatment, respectively.

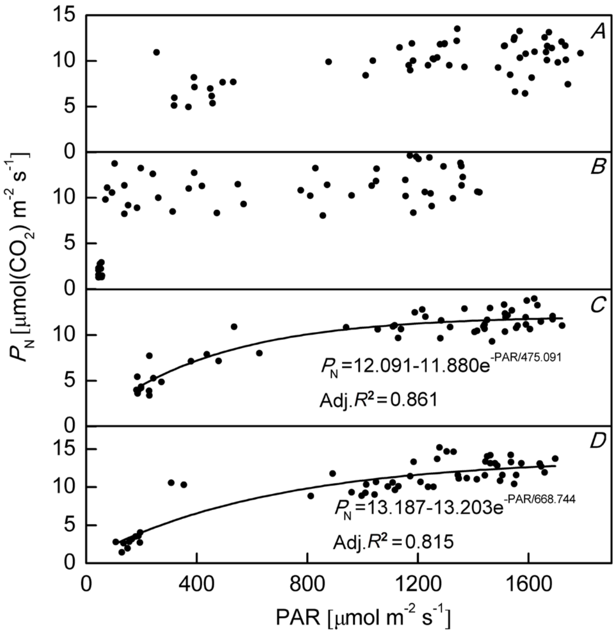

Fig. 3. The relationship between net photosynthetic rate (P_N) and photosynthetically active radiation (PAR) for control (*A*), pawpaw (*B*), Chinese toon (*C*), and walnut (*D*) plots. Lines describe the exponential relationship between P_N and PAR. Values are from four treatments (n = 55).

Discussion

Agroforestry system is a sustainable agricultural practice for highly efficient utilization of resources and can provide a suitable environment for crops. Land management by intercropping of crops has been extensively studied. The coffee, millet, and soybean farmers have benefited from this kind of land management (Perfecto *et al*. 1996, Sanou *et al*. 2012, Araújo *et al*. 2015, Nasielski *et al*. 2015). This land management is valid also for the cultivation of oil tree peony.

In situ patterns of leaf-level photosynthesis were created by interactions between an optimum ambient environmental conditions and the species-specific sensitivity to these combined factors (Braatne and Bliss 1999). The correlation analysis in this study showed that both similarities and differences were found in relationship between P_N and ecophysiological factors (Table 3). In all treatments, PAR and g_s positively and significantly correlated with P_N, while C_a did not show any correlation with P_N, indicating that environmental conditions may be similar surrounding the study species, but the photosynthetic responses of the species are different (Wu *et al*. 2011).

Economically, the results showed benefits and drawbacks of *P. ostii* grown in agroforestry systems in summer. The major benefits can be placed into two main categories, both associated with a reduced stress for the plant. Amelioration of microclimatic and site conditions, such as reduced T_{air}, PAR, and higher RH, promoted the morphological and physiological changes of *P. ostii* and increased the seed yield. Moderate shade within agroforestry systems can improve the efficiency of utilization of resources and microclimatic conditions within the systems, contributing to an overall high biomass production (Xue *et al*. 2008, Freese *et al*. 2010,

Table 2. Fluorescence parameters, chlorophyll contents, and SPAD value of *Paeonia ostii* in control, pawpaw, Chinese toon, and walnut plots. Values are means ± SD, n = 45. *The same letters* indicate no significant differences (P<0.05) according to the *Tukey*'s test. Chl – chlorophyll; ETR – electron transport rate; F_v/F_m – maximal quantum yield of PSII photochemistry; F_v'/F_m' – photochemical efficiency of PSII in the light; NPQ – nonphotochemical quenching; q_P – photochemical quenching coefficient; Φ_{PSII} – effective quantum yield of PSII photochemistry.

Parameter	Control	Pawpaw	Chinese toon	Walnut
F_v/F_m	0.75 ± 0.01^b	0.79 ± 0.01^a	0.80 ± 0.04^a	0.79 ± 0.01^a
F_v'/F_m'	0.45 ± 0.02^a	0.47 ± 0.03^a	0.46 ± 0.04^a	0.48 ± 0.02^a
Φ_{PSII}	0.29 ± 0.01^b	0.32 ± 0.03^{ab}	0.30 ± 0.03^{ab}	0.33 ± 0.023^a
ETR	121.41 ± 5.31^b	133.91 ± 12.39^{ab}	127.29 ± 13.91^{ab}	141.67 ± 12.73^a
q_P	0.64 ± 0.02^b	0.67 ± 0.01^{ab}	0.65 ± 0.02^b	0.69 ± 0.03^a
NPQ	1.60 ± 0.19^b	1.74 ± 0.08^{ab}	2.21 ± 0.16^a	2.11 ± 0.40^a
Chl *a* [mg g^{-1}(FM)]	1.03 ± 0.01^c	1.46 ± 0.03^a	1.46 ± 0.02^a	1.18 ± 0.04^b
Chl *b* [mg g^{-1}(FM)]	0.45 ± 0.01^b	0.65 ± 0.01^a	0.63 ± 0.01^a	0.46 ± 0.04^b
Chl (*a*+*b*) [mg g^{-1}(FM)]	1.47 ± 0.01^c	2.11 ± 0.04^a	2.09 ± 0.03^a	1.63 ± 0.06^b
Chl *a*/*b* ratio	2.29 ± 0.03^b	2.23 ± 0.06^c	2.32 ± 0.02^b	2.76 ± 0.29^a
SPAD value	45.67 ± 1.23^b	57.73 ± 1.46^a	54.60 ± 1.50^a	51.76 ± 0.90^b

Table 3. Correlation coefficients (R^2) for net photosynthetic rate (P_N) and environmental or physiological parameters of *Paeonia ostii* in control, pawpaw, Chinese toon, and walnut plots. *, ** – significant at $P<0.05$ and $P<0.01$, respectively; ns – not significant; df ($n = 55$). C_i – intercellular CO_2 concentration; E – transpiration rate; ETR – electron transport rate; g_s – stomatal conductance; RH – relative humidity; T_{air} – air temperature; T_{leaf} – leaf temperature; WUE – water-use efficiency.

Parameter	Control	Pawpaw	Chinese toon	Walnut
g_s	0.684**	0.880**	0.802**	0.519**
C_i	–0.075ns	–0.695**	–0.666**	–0.766**
E	0.625**	0.901**	0.820ns	0.609**
WUE	0.139ns	0.619**	–0.039ns	0.626**
T_{air}	0.492**	0.450**	0.055ns	0.787**
T_{leaf}	0.105ns	0.594**	0.849**	0.834**
C_a	0.263ns	–0.063ns	–0.028ns	–0.078ns
RH	–0.076ns	–0.462**	0.046ns	0.051ns
PAR	0.616**	0.605**	0.895**	0.887**
ETR	0.111ns	–0.092ns	0.065ns	0.119ns

Table 4. Correlation of SPAD value and chlorophyll (Chl) content of *Paeonia ostii* in control, pawpaw, Chinese toon, and walnut plots. *, ** – significant at $P<0.05$ and $P<0.01$, respectively; ns – not significant; df ($n = 55$).

Parameter	Control	Pawpaw	Chinese toon	Walnut
Chl *a*	–0.523ns	0.603ns	0.635ns	0.538ns
Chl *b*	–0.621ns	0.490ns	0.748*	0.664ns
Chl (*a*+*b*)	–0.705*	0.668*	0.687*	0.753*
Chl *a*/*b*	0.432ns	0.111ns	–0.658ns	–0.480ns

Zhang *et al*. 2011). The morphological characteristics (*e.g.*, thinner stem, bigger crown, and more green leaves) and yield indexes (*e.g.*, the higher pod number per plant, 1,000-seed mass, and harvest seed yield) were observed in Chinese toon and walnut treatments in comparison to monoculture. It has indicated that the involved systems could lead to allometry and regulate the relationship of distributive proportion between sink and source of *P. ostii* (Cao and Ohkubo 1998, Wang *et al*. 2017). The Chl fluorescence can be used to evaluate changes in PSII photochemistry of leaves. The normal F_v/F_m value, as the probe response to the extent of stress from environment, is in the range of 0.80–0.85 under nonstress conditions, while it could significantly decrease under stressful conditions (Lichtenthaler *et al*. 2007). The higher values of F_v/F_m were observed in agroforestry systems in comparison with the control treatment, indicating that photosynthesis of *P. ostii* was negatively influenced by full sunlight. The higher Φ_{PSII} and q_p in agroforestry systems suggested that agroforestry systems could enhance the light capture efficiency, the actual photochemical efficiency of PSII, the activity of electron transfer, and the efficiency of heat dissipation for *P. ostii* leaves (Müller *et al*. 2001, Cai *et al*. 2016). Higher NPQ means that higher part of absorbed light energy is dissipated by protective mechanisms (Gilmore 1997). However, higher NPQ in this study is observed in agroforestry system indicating that light-utilization efficiency decreased in photosynthetic process, and the underlying reason remains to be explored.

Reduction in the quantity and quality of transmitted light can avoid over-burning. Strong light tends to induce T_{air} to rise and RH to drop, which can inhibit photosynthesis and may lead to photooxidative destruction of the photosynthetic apparatus (Powles 1984, Valladares and Pearcy 2010). Evidence showed that moderate shade treatment could relieve 'midday depression of photosynthesis' for understory plants (Zhang *et al*. 2015, Huang *et al*. 2018). In this study, the obviously decreased P_N, which was observed in full sunlight at noon, was relieved in Chinese toon and walnut treatments. However, the reason why 'midday depression of photosynthesis' occurred in pawpaw treatments was different from the above, and it may be related to temporary decreased PAR at noon.

The main drawback was competition for light intensity in forest understory. The PAR in pawpaw, Chinese toon, and walnut treatments was 54.3, 82.0, and 81.0% of that in control treatment (full sunlight), respectively, but there was no significant difference in P_N, especially for pawpaw treatment, where relatively stable light conditions maintained stable photosynthesis (Fig. 2). On the other hand, it might be because the understory plant species utilize high-light sunflecks, which significantly contribute to the percentage of total carbon gain (Pfitsch and Pearcy 1989). In addition, shade leaves were relatively enriched in Chl *b* and have the lowered Chl *a*/*b* ratio, which has been thought to be a chromatic adaptation to help balance the light absorption between the two photosystems (Anderson 1986, Adamson *et al*. 1991). In pawpaw treatment, the highest Chl *a*, *b*, total Chl contents, and the lowest Chl *a*/*b*

Table 5. Growth and yield indexes of *Paeonia ostii* in control, pawpaw, Chinese toon, and walnut plots. Values are means ± SD, $n = 10$. *The same letters* indicate no significant differences ($P<0.05$) according to the *Tukey*'s test.

Parameter	Control	Pawpaw	Chinese toon	Walnut
Stem diameter[cm]	1.66 ± 0.05^a	1.11 ± 0.03^c	1.58 ± 0.06^{ab}	1.46 ± 0.06^b
Plant height[cm]	64.72 ± 2.17^a	70.32 ± 2.05^a	68.32 ± 2.05^a	65.93 ± 2.02^a
Crown width [cm]	66.80 ± 1.21^b	72.46 ± 1.01^a	70.21 ± 1.93^{ab}	67.65 ± 0.98^{ab}
Pod number per plant	2.57 ± 0.23^a	0.70 ± 0.12^b	2.93 ± 0.24^a	2.67 ± 0.31^a
1,000-seed mass [g]	309.46 ± 1.54^c	283.28 ± 0.78^d	343.60 ± 0.78^a	324.93 ± 0.77^b
Yield [kg ha^{-1}]	$1,924.34 \pm 53.53^c$	706.18 ± 46.26^d	$2,972.75 \pm 63.82^a$	$2,287.94 \pm 46.33^b$

ratio were observed. One could assume that the higher Chl content and suitable habitat are mainly responsible for the higher P_N; however, this is not the case. The possible reason could be that the shade effect was more adverse on fruit yield than that on photosynthetic capability and flowering stage, indicating effects on bud differentiation and fruit set (Cai 2011). In addition, long-term exposure to shade may diminish reproductive potential directly by decreasing floral initiation (Cannell 1975, Pang *et al*. 2017). Therefore, it was concluded that the pod and fruit set can both be affected by shading, which can directly reduce crop yield even if all the other growth factors are favorable. Compared to the other control treatments, the fewer pod and lower seed yield were observed in pawpaw treatment, whereas the P_N did not show any difference. The effect of agroforestry systems on seed yield of oil tree peony is possibly due to several factors such as reduced photosynthesis, an imbalance of biomass allocation between reproductive growth (*e.g*., flower initiation) and vegetative growth, and other morphogenetic characteristics.

Monoculture and intercropping system provide distinct environmental factors affecting leaf pigment composition and content. Hand-held Chl meters, nondestructive methods for determining leaf Chl content, present advantages by allowing rapid and repeated measurements of the same leaves overtime. In this study, higher SPAD values were observed in agroforestry system (Table 2), and there was a significant correlation between SPAD value and Chl (*a*+*b*) of *P. ostii* in agroforestry system (Table 4), which was consistent with Mielke *et al*. (2010). However, it also showed an opposite relationship in control indicating that the mathematical relationship between SPAD values and foliar pigment content varies with environmental growth conditions (Campbell *et al.* 1990).

Many factors can influence tree shading of adjoining agricultural crops within tree-based intercropping systems. Therefore, shade tree management (*e.g*., pruning, thinning, and/or replanting) is also essential to ensure the normal growth and development of understory plants. So further research on other aspects, *e.g*., allelopathy, soil organic matter, biological nitrogen fixation, and light availability of *P. ostii* within agroforestry systems are needed.

In summary, we found that there is a great potential for tree-based intercropping systems in Henan, a traditionally agricultural province of China, where *P. ostii* has long history of cultivation. Therefore, the study of the agroforestry system in Henan can play an important role in resolving the land contention between agriculture and forestry, increasing farmer's income, and promoting the sustainable and harmonious development between economy and environment. This study could be an important contribution to the science of land management in oil peony and other understory crops.

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